ANNALS
of CARNEGIE MUSEUM

PALEONTOLOGY AND GEOLOGY OF THE BADWATER CREEK AREA, CENTRAL WYOMING. PART 15. REVIEW OF THE LATE EOCENE PRIMATES FROM WYOMING AND UTAH, AND THE PLESITARSIIFORMES

Leonard Krishtalka
Assistant Curator, Section of Vertebrate Fossils

Abstract

New primate material from the late Eocene of Badwater allows documentation of the occurrence and systematics of seven species as follows: *Phenacolemur mcgrewi*; *P. shifrae* (new); *Trogolemur* sp.; *Macrotarsius siegerti*; *Chumashius* sp.; *Uintasorex* sp. cf. *U. parvulus*; *Mytonius hopsoni*. *Ourayia*, from the Uintan of Utah, is more strictly defined, with part of the hypodigm referred to *Macrotarsius jepseni* (new combination). The alleged microsyopid affinities of uintasoricines and some paromomyids are reviewed and not accepted. The relationships among plesiadapiform-tarsiiform primates are revised in accordance with inferred shared-derived similarities, and two major clades are recognized—all Plesiadapiformes (Plesiadapidae, Paromomyidae, Microchoeridae, and Anaptomorphidae) share the derived protocone fold on the upper molars; all Tarsiiformes (Omomyidae: Omomyinae, Uintasoricinae) are united in having continuous and parabolic protocristae on the upper molars enclosing a broad, shallow trigon basin.

Introduction

Since the last review of the late Eocene primates from the Badwater Creek area (Robinson, 1968), continued collecting from the Uintan (localities 5, 5A, 5 Front, 5 Back, Wood, 6) and Duchesnean (locality 20) deposits has yielded additional dental remains referrable to new and previously described taxa. It is clear that the Badwater sediments are not part of the Tepee Trail Formation (Krishtalka and Black, 1975; West et al., manuscript) although their formational status has not yet been determined.

Robinson (1968) described seven species of primates from Badwater—one as a paromomyid (*Phenacolemur mcgrewi*), four as omomyids (*Macrotarsius siegerti*, ?*Hemiacodon* sp., ?*Chumashius* sp.,
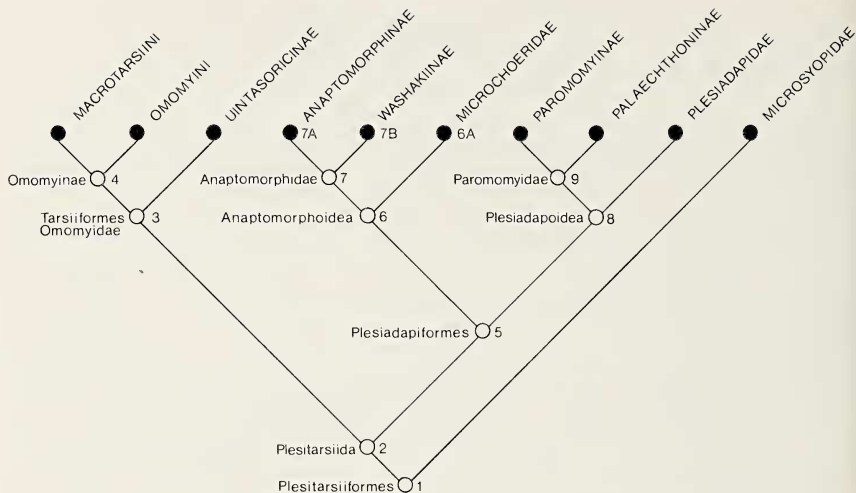
Fig. 1.—Hypothesized relationships among the major groups of plesiadapiform-tarsiiform primates (Plesitarsiiformes, Gingerich, 1976).

Node 1.—Incisors lost; canine develops and erupts at the front of the jaw and is followed by five premolars of which P_1^1 and P_3^3 may be inhibited, with retention of dP_1^1 and dP_3^3.

Node 2.—Paraconid and metaconid smaller on M_{2-3} than on M_1; talonid cusps, especially the hypoconulid, reduced on the lower molars; hypocristid on M_{1-2} flexed at a point labial to the midline of the molar.

Node 3.—Pre- and postprotocristae form a wide parabola on M^{1-3} enclosing a broad, shallow trigon basin; conules reduced; cingula on M^{1-2} extend around lingual face of the protocone; cristid obliqua on P_5M_1 are buccal to the midline of the tooth; hypoflexid notch shallow; entoconid and hypoconid flattened.

Node 4.—Low, weak, lingual ridge connects distinct and well-separated paraconid and metaconid on M_{1-3}.

Node 5.—Protocone fold on M^{1-2} continuous with postcingulum and enclosing posterointernal basin; M^{1-2} squared lingually, with longer lingual slope on protocone; talonid on M_{2-3} compressed.

Node 6.—Postprotocrista on M^{1-3} weaker and shorter and does not reach apex of protocone.

Node 6A.—P^5M^{1-3} more nearly quadrate; postcingulum extends lingually and ends in a broad-based hypocone, directly posterior to the protocone.

Node 7.—M^{1-2} more transverse; protocone with longer lingual slope and some distention of the lingual base; cristid obliqua on M_1 joins metaconid.

Node 7A.—M^2 enlarged and more transverse; apex of protocone on M^{1-2} occurs more labially so that the lingual slope of the protocone is much longer and the protocristae are much shorter; increased lingual distention of enamel on M^{1-2}; P_5 exodaenodont labially, taller than M_1; closely appressed paraconid and metaconid on M_{2-3} in marked contrast to M_1; talonid on M_{1-2} shorter.

Node 7B.—Postcingulum extends lingually and ends in conical hypocone posterolingual to protocone on M^{1-2}; protocone fold weak at junction with postcingulum that is marked by a weak cuspule or wear facet; precingulum ends in a pericone anterolingual to the protocone.

Node 8.—Upper canine cuspate; P_2 reduced; metacone and paraconule occur on P^5;

one sp. incertae sedis), and two as anaptomorphids (*Uintasorex* sp. cf. *U. parvulus*, ?*Trogolemur* sp.). In the same paper Robinson also discussed Uintan primates from Utah—*Ourayia uintensis*, *Hemiacodon jepseni* (new species), and *Mytonius hopsoni* (new genus and species), all omomyids.

Uintasorex has since been identified as a microsyopid (Szalay, 1969b; Bown and Gingerich, 1973; Bown and Rose, 1976) although, as discussed below, conclusions concerning the composition and affinities of this family are not without problems. The hypodigm of *Ourayia* has expanded and contracted with each review of the genus, and an attempt to clarify its systematics is made. Also, the anaptomorphids and omomyids as treated by various workers (Simons, 1972; Szalay 1976) do not appear to be monophyletic groups. Continued adherence to these taxonomic schemes precludes a rigorous reflection of the phylogenetic relationships among these taxa. A summary of a new and different view of relationships among the major taxa of Plesitarsiiformes (Gingerich, 1976), based on inferred shared-derived characters, is presented in Fig. 1. A more detailed treatment of all plesitarsiiform genera will appear elsewhere (Krishtalka and Schwartz, manuscript). Accordingly, among the primates recorded here, *Macrotarsius*, *Chumashius*, *Mytonius*, and *Ourayia* (Omomyinae) and *Uintasorex* (Uintasoricinae) are tarsiiforms. *Trogolemur* (Anaptomorphidae) and *Phenacolemur* (Paromomyidae) are plesiadapiforms. Microsyopids are provisionally included in plesitarsiiforms in agreement with Bown and Gingerich (1973), Bown and Rose (1976), and Gingerich (1976), but *pace* Szalay (1975, 1976).

Schwartz and Krishtalka (1976, 1977) have suggested that the antemolar dental complement of plesiadapiform-tarsiiform primates is a canine at the front of the jaw followed by five or fewer premolars. Premolars at the first and third loci may be retained deciduous teeth. This interpretation of dental homologies will be followed here.

←

metacone occurs on P^4; paraconid reduced on P_5M_{1-3}; trigonid quadrate on M_1, anteroposteriorly compressed on M_{2-3}; M_3 with prominent third lobe and double or large hypoconulid.

Node 9.—Rudimentary protocone on P^4; less robust lower canine; trigonid on M_{1-3} inclined anteriorly.

Included genera are as follows: Microsyopidae (*Cynodontomys*, *Microsyops*, *Craseops*, *Alsaticopithecus*); Plesiadapidae [*Pronothodectes* (*Elphidotarsius*, *Carpodaptes*, *Carpolestes*), *Nannodectes*, *Plesiadapis*, *Chiromyoides*, *Platychoerops*]; Paromomyidae [(*Palaechthon*, *Palenochtha*), (*Paromomys*, *Phenacolemur*, *Zanycteris*, *Picrodus*)]; Microchoeridae (*Nannopithex*, *Necrolemur*, *Microchoerus*, *Rooneyia*); Anaptomorphidae [(*Loveina*, *Shoshonius*, *Washakius*, *Hemiacodon*), (*Anemorhysis*, *Altanius*, *Pseudotetonius*, *Trogolemur*, *Absarokius*, *Anaptomorphus*, *Tetonius*)]; Omomyidae [(*Uintasorex*, *Niptomomys*, *Tinimomys*), (*Omomys*, *Macrotarsius*, *Ourayia*, *Mytonius*, *Tarsius*, *Chumashius*, *Uintanius*, *Pseudoloris*)].

Abbreviations in this paper are as follows: CM, Carnegie Museum of Natural History; PU, Princeton University; UCM, University of Colorado Museum; YPM, Yale Peabody Museum; L, length; W, width; PW, posterior width.

All measurements in text and in the tables are in millimeters. All photographs in the figures are scanning electron stereomicrographs.

Systematic Accounts

Family Paromomyidae

Phenacolemur Matthew, 1915

Bown and Rose (1976), in the latest review of this genus, resurrected *Ignacius* Matthew and Granger, 1921, to include *I. frugivorus*, *I. fremontensis*, and *I. mcgrewi*—species formerly assigned to *Phenacolemur* (Simpson, 1955; Robinson, 1968; Gazin, 1971)—and a new species, *I. graybullianus*. Retained in North American *Phenacolemur* are *P. praecox*, *P. citatus*, *P. jepseni*, *P. pagei*, and a new species, *P. simonsi*.

Among the many features listed in their diagnoses of the two genera (Bown and Rose, 1976:112, 114), only three appear to be truly diagnostic, that is, not shared. In contrast to *Phenacolemur*, *Ignacius* has the following characteristics: (1) a narrower and deeper mandible relative to the cheek teeth; (2) a V-shaped rather than anteroposteriorly straight centrocrista on the upper molars; and (3) smaller P_4^4 than M_1^1. However, a number of contradictions between this diagnosis and the morphology of the included species imply that the validity of *Ignacius* is open to question: (1) *I. mcgrewi* has anteroposteriorly aligned rather than V-shaped centrocristae on M^{1-2}—a characteristic of *Phenacolemur*. Neither P_4^4 nor the mandible of this species has been recovered as yet; (2) in *P. simonsi* the centrocristae are straight (*Phenacolemur*-like), but P_4^4 are smaller than M_1^1 (*Ignacius*-like) (Bown and Rose, 1976; Fig. 3b, Table III). The mandible of *P. simonsi* is unknown; (3) in *P. pagei* the centrocristae are straight and P_4 is larger than M_1 (*Phenacolemur*-like), but P^4 is smaller than M^1 (*Ignacius*-like).

If these species do constitute two genera, the diagnostic characters cited by Bown and Rose (1976) are unsatisfactory. *Ignacius* is here provisionally considered valid only on the basis of the V-shaped centrocristae on the upper molars, and thus includes only *I. fremontensis*, *I. frugivorus*, and *I. graybullianus*.

Since Robinson (1968) described *P. mcgrewi*, additional teeth of this and a new, smaller species have been recovered from the Badwater deposits.

Phenacolemur mcgrewi Robinson, 1968

Phenacolemur mcgrewi Robinson, 1968
Ignacius mcgrewi Bown and Rose, 1976

Holotype.—CM 15635, LM¹, locality 5 Front.
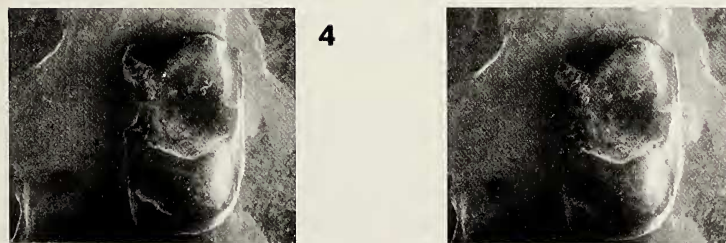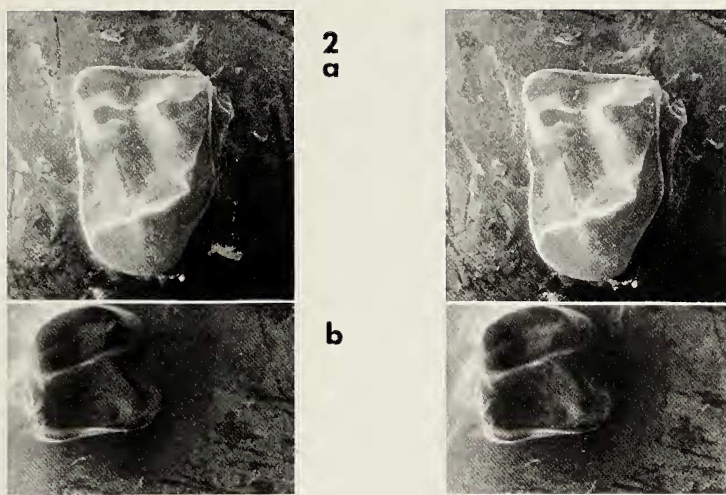
Fig. 2.—*Phenacolemur shifrae*, new species. (a) CM 15797, RM^2, holotype; (b) UCM 38323, RM$_2$; both approx. ×13.

Fig. 3.—*Mytonius hopsoni*. CM 15068, LM$_1$; approx. ×9.

Fig. 4.—*Chumashius* sp. CM 31275, RM^1; approx. ×9.

Referred specimens.—M_2: CM 29005, 15793, UCM 26012; M^1: CM 15795, 15796; M^2: CM 15794.

Localities.—5A, 5 Front, 6, 20; Badwater Creek area, Wyoming.

Known distribution.—Uintan and Duchesnean, Wyoming.

Emended diagnosis.—Known teeth (M^1, M_2^2) smaller than those of *P. praecox*, *P. citatus*, *P. jepseni*, larger than those of *P. simonsi*, but close in size to those of *P. pagei*. M^{1-2} less quadrate, more transverse (lower L/W ratios) with shallower posterointernal basins than North American species of *Phenacolemur* except *P. pagei*; M^1 lacks the mesostyle, the deep ectoflexus and strong ectocingulum of the latter; M_2 narrower in proportion to length than that of *P. pagei* and lower crowned.

Description and remarks.—Of the specimens originally assigned by Robinson (1968) to *P. mcgrewi* only the type (M^1, CM 15635) and an isolated M_2 (CM 26012) belong here. The smaller teeth he identified as second molars are referred below to a new species of *Phenacolemur*. New material of *P. mcgrewi* includes an M^2, which, except for its slightly shorter length, bears the morphology of M^1; the paracone is larger than the metacone; the postprotocingulum (=protocone fold) and postcingulum enclose a shallow posterointernal basin; the conules are evident as thickenings on the pre- and postprotocristae, with the paraconule slightly stronger.

Among North American species of *Phenacolemur*, *P. mcgrewi* most closely resembles the Tiffanian *P. pagei* in known parts of the dentition. M^1 of the two species is virtually identical except for a tiny mesostyle, a broader ectocingulum and deeper ectoflexus in the latter. M^2 of *P. pagei* lacks a mesostyle, but the ectocingulum and ectoflexus are stronger than on that of *P. mcgrewi*.

Phenacolemur shifrae, new species
(Fig. 2; Table 1)

Holotype.—CM 15797, RM^2, locality 6, Badwater Creek area, Uintan, Wyoming.

Referred specimens.—M^1: CM 15103, 15798; M^2: CM 14598, 15799; M_2: CM 21637, UCM 38323; M_3: CM 15726.

Localities.—5, 5A, 6, Badwater Creek area, Wyoming.

Known distribution.—Uintan, Wyoming.

Diagnosis.—Smallest known species of *Phenacolemur*.

Etymology.—Named for Shifra Krishtalka.

Description and remarks.—*P. shifrae* is closest in size to the Wasatchian *P. simonsi*, but M^{1-2} of the former are significantly shorter anteroposteriorly and more transverse (L/W ratio lower) and have weaker protocristae and postcingula, a smaller, shallower posteroin-

ternal basin, and shorter protocone fold. In these features *P. shifrae* most closely resembles *P. mcgrewi* and the Tiffanian *P. pagei*, although M^{1-2} of *P. shifrae* are significantly smaller. M_{2-3}, the only known elements of the lower dentition in *P. shifrae*, are slightly shorter and narrower than that of *P. simonsi*, and M_3 has a narrower third lobe.

The extremely similar morphology of M^{1-2} of *P. mcgrewi*, *P. shifrae*, and *P. pagei* may imply that these three species are the most closely related among known species of *Phenacolemur*. Their disjunct temporal distribution—absence of these or closely related species from the Wasatchian or Bridgerian record—is not particularly disturbing and does not mitigate against their apparently close relationship. *Phenacolemur* was long thought to have become extinct in the early Eocene until it was recovered from the Badwater Uintan deposits. Some species may have occupied habitats during the Eocene that were far from areas of deposition that account for currently preserved and sampled deposits. This bias of facies is also reflected in the record of Eocene multituberculates, rodents, dermopterans, some insectivores, and artiodactyls (Black, 1967, 1978; Krishtalka and Black, 1975; Krishtalka and Setoguchi, 1977).

<div align="center">

Family Anaptomorphidae

Trogolemur Matthew, 1909

Trogolemur sp.

</div>

Referred specimens.—M_1: UCM 26043; dP_5: CM 16019 (L, 1.8; PW, 1.3).

Localities.—5A, Wood.

Known distribution.—Uintan, Wyoming.

Remarks.—Robinson (1968) identified two isolated M_1s, CM 15066 and UCM 26043, as ?*Trogolemur* sp., an action corroborated by Szalay (1976) and this author. Unfortunately, one of these teeth, CM 15066, has since been lost. One diagnostic feature of P_5 and M_1 of *Trogolemur* is the posterior disposition of the metaconid and strong connection to the cristid obliqua. A Y-shaped groove separates the trigonid cusps on M_1.

The dP_5 thought to belong here bears this characteristic morphology. The semimolariform trigonid on CM 16019 is laterally compressed, with the paracristid linking a distinct protoconid and a tiny anterior paraconid. The metaconid, taller than the protoconid, is isolated from the trigonid but is joined to a steep cristid obliqua. The talonid is fully molariform. In size and crown morphology, the M_1 closely resembles that of the Bridgerian *T. myodes*, but referral of the Badwater material to this species must await recovery of a larger sample.

Table 1.—*Dimensions of teeth of* Phenacolemur mcgrewi *and* P. shifrae.

Catalog no.	M¹		M²		M₁		M₂		M₃	
	L	W	L	W	L	PW	L	PW	L	W
Phenacolemur mcgrewi										
CM 15635	2.0	2.8+								
CM 15795	2.0	—								
CM 15796	2.0	—								
CM 15794			1.8	2.9						
CM 29005					2.0	1.85				
CM 15793					2.0	1.8				
UCM 26012					2.0	—				
Phenacolemur shifrae										
CM 15103	1.4	2.0								
CM 15798	1.4	—								
CM 15797			1.3	2.0						
CM 14598			1.3	1.9						
CM 15799			1.2	1.9						
CM 21637							1.5	1.3		
UCM 38323							1.4	1.3		
CM 15726									1.9	1.1

Family Omomyidae

Type genus.—*Omomys* Leidy, 1869.

Included genera.—*Omomys, Chumashius, Macrotarsius, Tarsius, Pseudoloris, Uintanius, Tinimomys, Uintasorex, Niptomomys*, and, tentatively, *Mytonius* and *Ourayia*.

Known distribution.—Wasatchian to Chadronian, North America; Lutetian, Europe; Recent, Asia.

Emended diagnosis.—Tarsiiform primates (Fig. 1, node 3) with widely parabolic pre- and postprotocristae on M¹⁻³ that enclose a broad, shallow trigon basin; cristid obliqua on P_5M_{1-3} originates buccal to the midline of the tooth so that the hypoflexid notch is shallow; entoconid and hypoconid flattened on lower molars.

Subfamily Omomyinae

Type genus.—*Omomys* Leidy, 1869.

Included genera.—*Omomys, Chumashius, Macrotarsius, Tarsius, Pseudoloris, Uintanius*, and, tentatively, *Ourayia* and *Mytonius*.

Known distribution.—Wasatchian to Chadronian, North America; Lutetian, Europe; Recent, Asia.

Emended diagnosis.—Omomyid primates (see above and Fig. 1, node 4) in which the paraconid and metaconid on M_{1-3} are distinct and separate but are joined lingually by a weak crest. A morphocline

among members of this subfamily involves the progressively more an-
teromedial occurrence of the paraconid on M_{1-3}.

Ourayia Gazin, 1958

In the twenty years since *Ourayia* was named, it has had a mercurial
taxonomic history. Gazin (1958) correctly separated *Ourayia uintensis*
from Wortman's (1904) *Omomys*, with AMNH 1899, a partial right
dentary with $P_4P_5M_1M_2$, from the Uintan (Uinta B) of Utah, as the
type. Simons (1961) then allocated to *Ourayia* a mandibular fragment
with M_1 (AMNH 1900, Uinta B, Utah), paired dentaries and associated
palate (PU 16431, White River Pocket, Uinta B, Utah), and a second
set of paired dentaries (PU 11236, Kennedy's Hole, Uinta B, Utah).
Robinson (1968) disagreed with Simons and identified PU 16431 and
PU 11236 as a new species of *Hemiacodon*, *H. jepseni*. At the same
time he named a new genus and species, *Mytonius hopsoni*, from a
partial right dentary with P_5–M_2 (YPM 15266) and an isolated M_2 (CM
12309), both from Myton Pocket, Uinta C, Utah. Szalay (1976), in the
most recent review of *Ourayia*, concurred with Simons, reassigned PU
16431 and PU 11236 to *O. uintensis* and added YPM 15266 and CM
12309 to the species, thus synonymizing *H. jepseni* and *M. hopsoni*
with *O. uintensis*. In these studies reconstructions of *Ourayia*'s rela-
tionships involved either *Hemiacodon*, *Omomys*, or *Macrotarsius*.

Except for Gazin's and Robinson's analysis, diagnostic criteria on
the type of *Ourayia* have been overlooked. On AMNH 1899 P_4 is much
taller than P_5; the P_5 paraconid is not a distinct cusp but forms the
bulge-like anterior end of a strong paracristid; M_1 becomes much
broader posteriorly and the cristid obliqua originates buccally, below
the apex of the protoconid; M_2, with a strong labial cingulid and an-
teroposteriorly compressed trigonid is more nearly square in occlusal
outline than M_1; the buccal contour of M_{1-2} is not emarginate between
talonid and trigonid; a distinct paraconid is not discernible on M_2 in
the convex protoconid-metaconid crest that forms the leading edge of
the trigonid, although one may have occurred on an unworn molar;
the cristid obliqua on M_2 originates more labially from the posterior
face of the protoconid than on M_1, resulting in a shallower hypoflexid
notch; on M_{1-2} the hypoconulid is merely a median flexure of the hy-
pocristid.

Accordingly, comparison of PU 11236 with AMNH 1899 leaves no
doubt that the paired partial dentaries from the Kennedy's Hole lo-
cality are referrable to *Ourayia uintensis*. PU 11236 adds to our knowl-
edge of *Ourayia* the nature of unworn M_2, the morphology of M_3 and
the alveoli anterior to P_4. On M_{2-3} of PU 11236 a nubbin-like paraconid
occurs close to the metaconid and is part of the arcuate protoconid-
metaconid crest, so that the trigonid of these molars is closed lingually.

The absence of an M_2 paraconid on the type of *Ourayia*, AMNH 1899, is clearly due to wear. The hypoconulid lobe on M_3 of PU 11236 is short and the metaconid on M_{2-3} is reduced in comparison to M_1.

Contrary to Robinson's (1968) conclusion, PU 11236 differs generically from *Hemiacodon*. Unlike *Ourayia* (AMNH 1899, 1900, PU 11236), M_{1-3} of *Hemiacodon* are significantly more angular in occlusal outline, especially along the buccal margin of the crown, and the talonid and trigonids cusps are higher. The cristid obliqua on M_{1-2} of *Hemiacodon* originates lingually from the posterolingual part of the base of the metaconid, resulting in a deeper hypoflexid notch, especially on M_2. On M_2 of *Hemiacodon* the metaconid is not reduced and the trigonid is open lingually, because the paraconid is strong and separate from the metaconid. The hypoconulid lobe on M_3 of *Hemiacodon* is much longer.

The affinities of PU 16431, the palate and paired dentaries from White River Pocket, Utah, are likewise clear upon comparison to AMNH 1899 and PU 11236, type and referred material of *Ourayia*. Unlike *Ourayia*, on PU 16431 the P_4 is equal in height to P_5, the paraconid is strong and separate on M_2, the trigonid is not compressed, the paracristid is straight and the metaconid is not reduced. M_3 on PU 16431 is longer due to a well developed hypoconulid lobe. The features of P_5 and the lower molars that differentiate PU 16431 from *Ourayia* are shared with *Hemiacodon*. However, M_{1-3} of PU 16431 are equally distinct from *Hemiacodon* in occlusal outline (less angular, non-emarginate buccal contour, more nearly quadrate), position of the cristid obliqua (originates labially below protocone), and in having a shallow hypoflexid notch—features that PU 16431 shares with *Ourayia*. PU 16431 is distinct from both *Ourayia* and *Hemiacodon* in the structure of P_{4-5}—both premolars are shorter due to a shorter talonid and also on P_5 to a more triangular, molariform trigonid. The paraconid on P_5 is distinct cusp rather than part of a crest and occurs anterolingual rather than directly anterior to the protoconid. Additionally, the metaconid on M_{1-3} of PU 16431 is more bulbous and bears a sharp vertical crest, or cutting edge, on its posterior face. Upper molars of PU 16431 are even more distinct from those of *Hemiacodon*; they are more nearly quadrate (rather than transversely elongate), their posterior borders are not emarginate, their stylar areas are larger and bear a mesostyle and separate anterior and posterior ectocingula. Comparison with *Ourayia* is not possible because the upper dentition of the latter is not known.

The associated upper and lower dentitions of PU 16431 are virtually identical to those of *Macrotarsius*. Indeed, features previously cited by Szalay (1976) and Robinson (1968) as diagnostic of *Macrotarsius* correspond to the ones listed above in distinguishing PU 16431 from

Ourayia and *Hemiacodon*. PU 16431 is referred below to a new species of *Macrotarsius*.

Identification of YPM 15266 and CM 12309, Robinson's (1968) type and referred specimens of *Mytonius hopsoni*, is more difficult, because a diagnostic part of M_2 on YPM 15266—the lingual half of the trigonid—is broken away and with it knowledge of the metaconid and paraconid. Thus Robinson's association of CM 12309, a complete M_2, with YPM 15266 is not at all certain. Compared to *O. uintensis* (AMNH 1899, AMNH 1900, PU 11236) P_5 on YPM 15266 is shorter and broader, the metaconid is extremely weak and the cristid obliqua is medial rather than buccal. On M_1 the protoconid is more medial and the metaconid is more posterior than on M_1 of *Ourayia* resulting in a more oblique orientation of the posterior edge of the trigonid. YPM 15266 appears to be distinct from *O. uintensis*, whereas CM 12309 is not. Until more complete material is recovered it seems prudent to retain YPM 15266 as the type of *Mytonius hopsoni* rather than an extreme variant of *Ourayia*. Other material from Badwater and the Chadronian of South Dakota are also referable to *M. hopsoni*, as described below.

Ourayia uintensis (Osborn, 1895)

Microsyops uintensis Osborn, 1895
?*"Microsyops" uintensis* Osborn, 1902
Omomys uintensis Wortman, 1904
Ourayia uintensis (Osborn, 1895) Gazin, 1958
Ourayia uintensis (Osborn, 1895) Simons, 1961, in part
Hemiacodon jepseni Robinson, 1968, in part
Mytonius hopsoni Robinson, 1968, in part
Ourayia uintensis (Osborn, 1895) Szalay, 1976, in part

Holotype.—AMNH 1899, partial right dentary with $P_{4-5}M_{1-2}$, from White River Pocket, Uinta B, Utah.

Referred specimens.—AMNH 1900, PU 11236, CM 12309.

Localities.—Kennedy's Hole, White River Pocket and Myton Pocket, Uinta Formation, Utah.

Known distribution.—Uintan, Utah.

Emended diagnosis.—P_4 higher than P_5; P_5 trigonid with anterior, bulge-like paraconid and discrete metaconid, talonid short with buccal cristid obliqua; cristid obliqua on lower molars originates buccally on posterior face of protoconid; M_2 paraconid tiny nubbin on arcuate protoconid-metaconid cristid; buccal border of lower molars not emarginate; talonid much broader than trigonid on M_1; M_2 quadrate with low, flat talonid cusps; hypoconulid lobe on M_3 short.

Discussion.—*O. uintensis* is the only known species of the genus. Without knowledge of its upper dentition, any conclusions concerning the relationships of *Ourayia* are tentative. Based on the lower dentition

alone, *Ourayia* appears to be an omomyid and most closely related to *Macrotarsius*. M_{1-2} of *Ourayia* and *Macrotarsius* are derived in their quadrate occlusal outline, non-emarginate buccal contour and in the extreme buccal position of the cristid obliqua.

The alveoli anterior to P_4 are well preserved on the partial right dentary of PU 11236. The crown of the anteriormost tooth is broken away, but the base is large, laterally compressed and caniniform, and, as in all Plesitarsiiformes, is identified as a canine (Schwartz and Krishtalka, 1976, 1977; Schwartz, in press; Krishtalka and Schwartz, manuscript). The shape and position of the three alveoli between C_1 and P_4 imply that these bore single-rooted teeth, here dubbed $dP_1P_2dP_3$. Whether the first and third premolars were retained deciduous teeth is not certain. The alveolus for dP_1 is rectangular and compressed anteroposteriorly, whereas that for P_2 is much larger and oval. The dP_3 alveolus, also oval, is smaller than that for P_2 but slightly larger than that for dP_1. This pattern of alveolar size—P_2 larger than dP_1 or dP_3—is common among plesitarsiiforms that have these teeth.

Mytonius Robinson, 1968

Mytonius hopsoni Robinson, 1968
(Fig. 3; Table 2)

?*Hemiacodon* sp. Robinson, 1968
Mytonius hopsoni Robinson, 1968, in part
Ourayia uintensis Szalay, 1976, in part
Macrotarsius? sp. Szalay, 1976

Holotype.—YPM 15266, partial right dentary with P_5–M_2, from Myton Pocket, Uinta Formation (Uinta C), Uintan of Utah.

Referred specimens.—M_1: CM 15068; partial right dentary with P_5–M_1: CM 10855.

Localities.—5A, Badwater Creek area, Wyoming (CM 15068); Short Pine Hills, South Dakota (CM 10855).

Known distribution.—Uintan, Utah and Wyoming; Chadronian, South Dakota.

Emended diagnosis.—P_5 shorter and broader than *Ourayia*, with complete buccal cingulid and more medial cristid obliqua; metaconid weak on posterolingual face of protoconid. P_5 trigonid more premolariform than in *Macrotarsius*. M_1 trigonid more laterally compressed, with a more medial protoconid and posterior metaconid than in *Ourayia* and *Macrotarsius*.

Remarks.—The three specimens referred here seem, at least tentatively, to represent a single species. As noted in other sections, CM 15068 from Badwater does not resemble M_1 of *Hemiacodon* (Robinson, 1968) and certainly not M_1 of *Macrotarsius* (Szalay, 1976). CM 10855 also differs significantly from P_5–M_1 of *Macrotarsius* and strict definition of *Ourayia* (*pace* Szalay, 1976) excludes YPM 15266.

Chumashius Stock, 1933

Chumashius sp.
(Fig. 4)

Referred specimens.—M_1: CM 15069; M^1: CM 31275, 28827; M^3: CM 16011, 28641.

Localities.—5A, Wood, Badwater Creek area, Wyoming.
Known distribution.—Uintan, Wyoming.
Remarks.—Robinson (1968) correctly identified an isolated M_1 (CM 15069) as ?*Chumashius* sp.—a record omitted by Szalay (1976) in his review of the genus. Four more isolated teeth—two partial M^1s and two M^3s—also closely resemble *Chumashius*, but the material is too poor to be assigned confidently to *C. balchi*.

Like *Omomys*, *Macrotarsius*, and other tarsiiforms (Fig. 1, node 3) upper molars of *Chumashius* bear the derived widely divergent or parabolic protocristae that enclose a broad, shallow trigon basin. *Chumashius* is an omomyine in that the paraconid on the lower molars occurs medially rather than lingually. In both *Chumashius* and *Pseudoloris* the paraconid is closer to the protoconid than the metaconid on M_{1-3}.

Macrotarsius Clark, 1941

Three species of *Macrotarsius* are recognized here—the type species, *M. montanus*; *M. siegerti*, from Badwater, and a new species, *M. jepseni*, from the Uintan of Utah. *M. montanus* (Clark, 1941) is known only from the type, CM 9592, a partial right dentary with P_3, P_5-M_3. Robinson (1968) and Szalay (1976) list difference in size as the lone diagnostic criterion distinguishing *M. siegerti* from *M. montanus*. Although comparable teeth of *M. montanus* are consistently slightly longer or wider than those in the sample of *M. siegerti*, statistically, the difference in size is on the order of intraspecific variation. Known parts of the dentition differ significantly only in crown shape; P_5-M_3 of *M. montanus* are more bulbous (exodaenodont) labially.

Macrotarsius siegerti Robinson, 1968
(Figs. 5, 6, 7; Tables 2, 3)

Holotype.—CM 15122, RP_5, locality 5A, Badwater Creek area, Uintan, Wyoming.

Referred specimens.—P_4-P_5: CM 15800; P_5-M_1: CM 21990; P_5: UCM 26009; M_1: CM 16063, 16809, 15072, 28825; M_2: CM 15147; M_3: CM 14601, 15674, 19761; P^5-M^3: CM 18646; M^{1-3}: CM 14549, 15056; M^{2-3}: CM 15052; P^5: (tentatively) CM 15610, 15717; M^3: CM 28826.

Localities.—5, 5A, 5 Front, 5 Back, 6, Wood.
Known distribution.—Uintan, Wyoming.
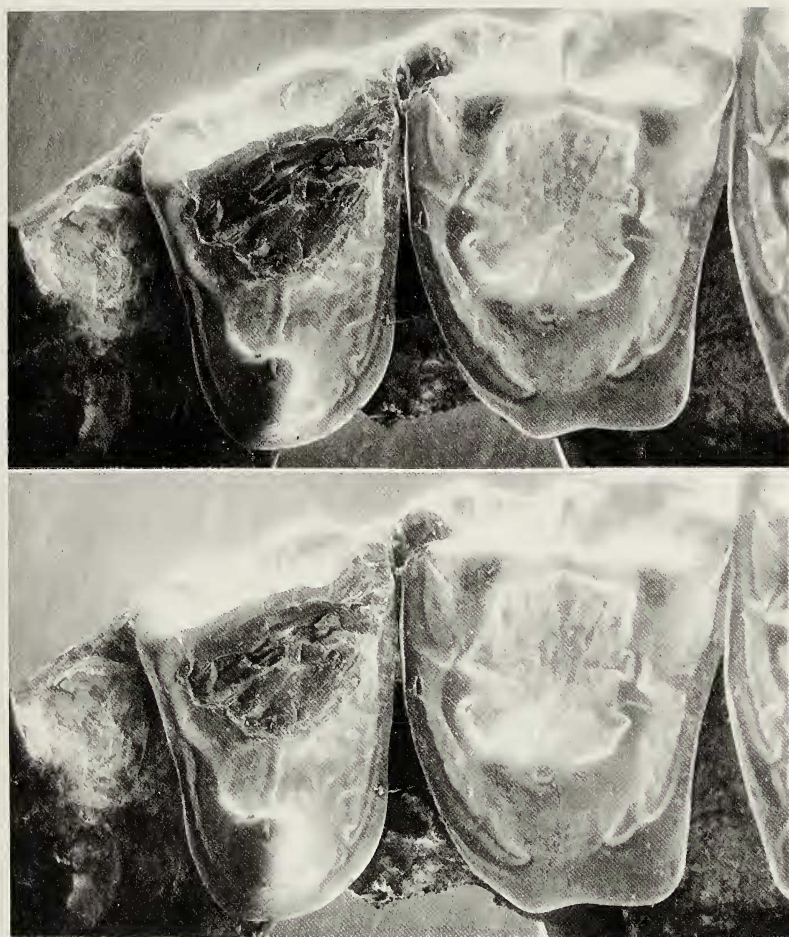*Description and remarks.*—The morphology of the known parts of

Table 2.—*Dimensions of lower teeth of* Macrotarsius montanus, M. siegerti, M. jepseni, Ourayia uintensis, *and* Mytonius hopsoni.

Taxa and no. of specimens	P_3		M_1		M_2		M_3	
	L	W	L	PW	L	PW	L	PW
Macrotarsius montanus	3.2	3.2	4.6	4.1	4.6	4.0	5.7	3.7
N	1	1	1	1	1	1	1	1
Macrotarsius siegerti	3.2–3.4	2.8–2.9	4.0–4.6	3.4–3.7	4.4	3.6	4.9–5.2	3.3–3.3
N	4	4	4	4	1	1	2	3
Macrotarsius jepseni	2.9–3.0	2.5	4.0	3.4	4.1	3.5–3.6	5.0	3.1
N	2	2	1	1	2	2	1	1
Ourayia uintensis	3.5–3.6	2.4–2.5	4.1–4.3	3.1–3.5	3.9–4.0	3.4–3.7	4.5	3.0–3.1
N	3	3	2	3	3	3	2	2
Mytonius hopsoni	2.7–3.0	2.4–2.7	3.5–3.8	3.0–3.1	3.5	3.5	—	—
N	2	2	3	2	1	1		

Table 3.—*Dimensions of upper teeth of* Macrotarsius siegerti *and* M. jepseni.

Taxa and no. of specimens	P^5		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W
Macrotarsius siegerti	2.9–3.2	3.8–4.6	4.0–4.2	5.1–5.2	4.0–4.2	5.3–5.4	3.0–3.7	4.8–5.2
N	3	3	3	4	4	3	3	4
M. jepseni	2.9	3.8	3.8	4.8	3.9	5.1	3.4–3.5	4.6–4.7
N	2	2	2	2	2	2	2	2

Fig. 5.—*Macrotarsius siegerti*. CM 18646 (part), LP^5–M^1; approx. ×11.

the lower dentition of *Macrotarsius* was adequately described by Clark (1941), Robinson (1968), and Szalay (1976). Four additional aspects, however, deserve comment.

(1) A recently recovered specimen of *M. siegerti*, CM 15800, preserves a number of premolars and the anterior part of the dentary including the symphyseal area and all alveoli. The shape and position of these alveoli are identical to those on CM 9592, type of *M. montanus*. The first alveolus, extremely large and laterally compressed, opens anterodorsally and on CM 9592 contains an enlarged tooth that

Fig. 6.—*Macrotarsius siegerti*. CM 18646 (part), LM$^{2-3}$; approx. ×11.

typically is the anteriormost, usually caniniform, tooth in known plesiadapiform-tarsiiform primates (Schwartz and Krishtalka, 1976, 1977). The next alveolus is tiny and contained a single-rooted tooth. The following alveolus is larger, oval, and in CM 9592, is occupied by a worn, single-rooted premolar. Behind this tooth is an alveolus for another single-rooted tooth, followed by two double-rooted premolars. The suggested lower antemolar dental complement of *M. siegerti* and
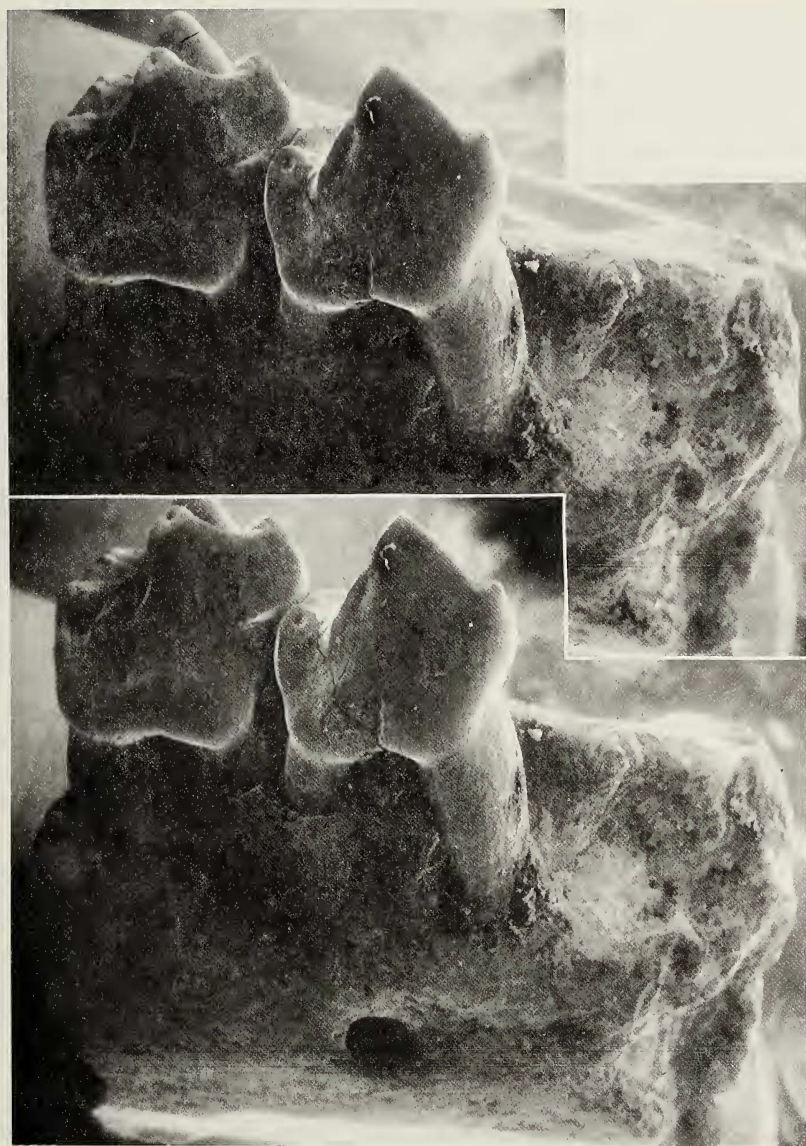
Fig. 7.—*Macrotarsius siegerti*. CM 15800, partial right dentary with P_{4-5} and alveoli for C, dP_1, P_2, dP_3; approx. ×12.

M. montanus is a canine and five premolars or, more specifically, $CdP_1P_2dP_3P_4P_5$.

(2) Two significant features were omitted by Szalay (1976) from his comparison of *Macrotarsius* and *Ourayia*—in *Macrotarsius*, a more molariform trigonid on P_5 and a separate paraconid and open trigonid on M_2. The paraconid on P_5 of *Ourayia* occurs nearly directly anterior to the protoconid, with a high cristid linking the two cusps; the P_5 paraconid of *Macrotarsius* is closer to the metaconid and anterolingual to the protoconid so that the three cusps form a V-shaped trigonid. P_4, broken on CM 9592, but complete on CM 15800, is lower and similarly more molariform than that of *Ourayia*. The trigonid, longer and narrower than the talonid, bears a low protoconid, a small paraconid, and a strong cristid on the posterior face of the protoconid. P_4 of *Ourayia* is longer and narrower than that of *Macrotarsius*, bears a higher protoconid and lacks a paraconid.

(3) CM 15068 (L, 3.7; PW, 3.0), a left M_1, was identified as ?*Hemiacodon* sp. by Robinson (1968) and as *M. siegerti* by Szalay (1976), but falls well below the range in size of M_1 of *M. siegerti* (Szalay, 1976:288, Table 18). M_1 of *Macrotarsius* characteristically has a lingually bulbous metaconid and hypoconid, a vertical cristid (=cutting edge of Szalay, 1976) along the posterior face of the metaconid and lacks a labial cingulid. In contrast to *Macrotarsius* but like *Ourayia* and *Mytonius*, the lingual face of the crown is not bulbous on CM 15068, the cristid on the posterior face of the metaconid is absent, and a cingulid occurs along the labial contour of the crown. CM 15068 resembles *Mytonius* and differs from *Ourayia* in its more laterally compressed trigonid—the protoconid is more medial and the metaconid more posterior.

(4) Szalay (1976:287, Fig. 78) alluded to a Chadronian record of ?*Macrotarsius* sp. from CM 10855, a partial right dentary with P_5 and a broken M_1 from the Short Pine Hills, South Dakota, although neither the specimen nor the taxon is mentioned in text. P_5 on CM 10855 is more premolariform (weak metaconid, no distinct paraconid) than that of *Macrotarsius*, much shorter and wider and with a lower protoconid than that of *Ourayia*, but is most similar to that of *Mytonius hopsoni* (YPM 15266) as is the preserved remnant of M_1.

Upper teeth known in *M. siegerti* are P^5–M^3 and these, especially M^3, exhibit a noteworthy range of variation. P^5 is triangular and transverse in occlusal view, with a well-developed postcingulum and a parastylar ectocingulum. Unfortunately, much of P^5 is broken away on CM 18646 [*pace* Szalay's illustration (1976:291, Fig. 81) of a complete P^5, which, although not noted as such, is a reconstruction]. Two isolated P^5s (CM 15717 and CM 15610) identified as *Macrotarsius* by Robinson (1968) and Szalay (1976) are less transverse than P^5 on CM

18646 and lack the ectocingula on the latter. These are tentatively retained in *M. siegerti*.

M^{1-3} of *M. siegerti*, though quadrate in occlusal outline, are wider than long and longer labially than lingually. Paracone and metacone are robust and pyramidal with strong cristae. The protocone is broad and bears strong pre- and postprotocristae that form a parabola enclosing a broad trigon basin. A mesostyle, at the anterior end of a metastylar ectocingulum, is joined by a crest to the medial apex of the centrocrista. A parastylar ectocingulum, weaker than its metastylar counterpart, does not make contact with the mesostyle. The conules are poorly developed, with the paraconule slightly larger. The pre- and postcingula are strong and terminate lingually in a tiny pericone and hypocone, respectively. The degree of development of the ectocingula, mesostyle, pericone and hypocone varies considerably from CM 18646 (strong) to CM 14549 (extremely weak); the remainder of the hypodigm is intermediate in the expression of these characters. M^3 on CM 14549 is more nearly triangular than quadrate, because the posterolingual corner of the crown is not expanded posteriorly.

Macrotarsius jepseni (Robinson, 1968)

Ourayia uintensis Simons, 1961, in part
Hemiacodon jepseni Robinson, 1968, in part
Ourayia uintensis Szalay, 1976, in part

Holotype.—PU 16431, palate with upper dentition except left P^2, paired partial dentaries with left C, P_{4-5}, M_{1-3} and right C, P_4, M_{1-3}; from White River Pocket, Uinta Formation, Utah.

Known distribution.—Uintan, Utah.

Diagnosis.—Compared to *M. siegerti*, mesostyle on M^{1-3} small, not connected to centrocrista; P^5 less transverse. Compared to *M. siegerti* and *M. montanus*, P_1 alveolus unreduced, P_{1-3} alveoli more widely spaced, diastema between P_3 alveolus and P_4, $P_{4-5}M_{1-3}$ not exodaenodont buccally.

Description and remarks.—Unlike *M. siegerti*, the mesostyle on M^{1-3} of *M. jepseni* is not linked to the median flexure of the centrocrista. Otherwise the upper molars of both species are identical in crown morphology. As in *M. siegerti* and *M. montanus* the alveolus for P_2 in *M. jepseni* is larger than that for P_3 and the latter is larger than that for P_1. However in the two former species the P_1 alveolus is tiny and lingually displaced, the P_{1-3} alveoli are crowded and adjacent anteroposteriorly, and there is no diastema between the alveoli for P_3 and the anterior root of P_4. In contrast, the P_1 alveolus in *M. jepseni* is oval and unreduced, the alveoli for P_{1-3} do not border one on the other and a distinct diastema occurs between P_3 alveolus and P_4. Although the length along the dentary from the symphyseal border to the pos-

terior tip of M_3 is equal in *M. jepseni* and *M. montanus*, the posterior premolars and molars of the latter are larger—a condition made possible by the inferred crowding of the anterior premolars and reduction of P_1. $P_{4-5}M_{1-3}$ of *M. montanus* and *M. siegerti* are also broader than those of *M. jepseni* due to the buccal exodaenodonty of these teeth.

Apart from these differences, which in total imply specific distinction for this material from Utah, PU 16431 exhibits the shared-derived features of *Macrotarsius*—molariform trigonid on P_5; broad, quadrate molars with a mesostyle on a posterior ectocingulum on M^{1-3}; a vertical crest on the posterior face of the metaconid on M_{1-3}. *M. montanus* and *M. siegerti* are derived with respect to *M. jepseni* in the crowding of the anterior lower premolars, the extreme reduction and lingual displacement of the P_1 alveolus, the buccal exodaenodonty of $P_{4-5}M_{1-3}$, and the connection of the mesostyle to the centrocrista on M^{1-3} (known only in *M. siegerti*).

PU 16431 adds the morphology of the lower canine and teeth anterior to P^5 to our knowledge of *Macrotarsius*. The crown of the lower and upper canine is semispatulate, without digitations and, on the former, has a raised internal margocristid (Gingerich, 1976). P^1 is a trenchant, laterally compressed blade that is almost as large as the upper canine. Its large single root appears to be the result of fusion of two roots. P^2 and P^3 are subequal, single-rooted, smaller than P^1 but, like the latter, are trenchant blades with a tiny posterobasal cuspule. P^4, triangular in occlusal view, is narrower than P^5 and bears a high paracone that occupies most of the crown and a small lingual protocone.

On PU 16431 a premolariform tooth is glued to the anterior root of P_4 that forms the anterior edge of the specimen. The association of this alleged P_3 with PU 16431 is highly questionable; the alveolus for RP_3 is not preserved and the tooth is black, whereas all the teeth that are undoubtedly part of PU 16431 are brown.

Subfamily Uintasoricinae

Uintasoricinae Szalay, 1969*b*.
Uintasoricinae Bown and Rose, 1976, in part.

Type genus.—*Uintasorex* Matthew, 1909
Included genera.—*Uintasorex, Tinimomys, Niptomomys*.
Known distribution.—Wasatchian to Uintan, North America.
Emended diagnosis.—Tiny omomyids with enlarged P_5^5, semimolariform P_5, absence of premolars at P_1 and P_3 loci, paraconid reduced or absent on M_{2-3}.
Remarks.—*Uintasorex, Niptomomys,* and *Tinimomys* share the omomyid tarsiiform condition (Fig. 1, node 3) of parabolic protocristae on the upper molars that demarcate a broad, shallow trigon basin. The

cristid obliqua on the lower molars originates labially, below the pro-
toconid, so that the hypoflexid notch is shallow. As omomyids, these
three genera constitute the Uintasoricinae and are most closely related
to their sister group, the Omomyinae.

Identification of uintasoricines as tarsiiforms is contrary to recent
discussions of their affinities (Szalay, 1969b; Bown and Gingerich,
1972, 1973; Bown and Rose, 1976), although McKenna (1960) recog-
nized the similarities between *Niptomomys* and omomyids. Szalay
(1969b) erected the Uintasoricinae for *Uintasorex* and *Niptomomys*
and included the subfamily in the Microsyopidae. Earlier, Szalay
(1969a) had tentatively referred the microsyopids to Primates, included
the North American genera *Microsyops*, *Craseops*, and *Navajovius*
(tentatively) in the family and considered *Cynodontomys* a junior syn-
onym of *Microsyops*.

Among the diagnostic criteria of *Microsyops* are on M^{1-2} a hypocone
at the lingual end of a postcingulum and lack of a protocone fold
(=postprotocingulum of Bown and Gingerich, 1973) and on M_{1-3} a deep
notch between the proximal and unreduced hypoconulid and entoco-
nid.

At this time the Paromomyidae included, among others, the Paleo-
cene genera *Plesiolestes*, *Palaechthon*, *Palenochtha*, and *Torrejonia*.
These are characterized in part by absence of a hypocone, presence
of a protocone fold that is continuous with the postcingulum on M^{1-2},
and a crest between the hypoconulid and entoconid.

As primates or non-primates [Szalay (1975, 1976) has since reversed
his opinion] the microsyopids are accorded primitive status on the
basis of an entotympanic bulla and medial entocarotid artery in *Mi-
crosyops* (Szalay, 1969a). If the microsyopids were primitive Eocene
primates, where did their ancestry lie? Bown and Gingerich (1973)
suggested that a *Plesiolestes* (Paleocene)-*Cynodontomys* (Eocene) lin-
eage provided the answer, after detailed comparisons of the dentitions
of the two genera. One apparent inconsistency is their unexplained
recognition of both *Cynodontomys* and *Microsyops* subsequent to Sza-
lay's synonymy of the two genera. A second is the necessary loss of
the protocone fold and hypoconulid-entoconid crest and appearance
of a hypocone and a notch between a twinned hypoconulid and ento-
conid in the *Plesiolestes*-*Cynodontomys* transition—two important al-
leged evolutionary events that Bown and Gingerich (1973) say, but do
not demonstrate, are functionally related.

In the same issue of that journal Szalay (1973) described a new
Paleocene paromomyid (*Micromomys*), a new species of *Plesiolestes*
(*P. sirokyi*) and synonymized *Torrejonia* (Gazin, 1968) with *Plesi-
olestes*. Most recently, Bown and Rose (1976) reclassified the Micro-
syopidae to include the four above mentioned paromomyids (*Plesi-

olestes, *Palaechthon*, *Palenochtha*, *Torrejonia*) in the Microsyopinae and outlined the inferred relationships between microsyopines and uintasoricines. Here *Cynodontomys* is considered a junior synonym of *Microsyops* and *Torrejonia* is listed as a valid genus without mention of Szalay's relegation of that taxon to *Plesiolestes*. Their diagnosis of the Microsyopinae (including, among others, *Microsyops*, *Plesiolestes*, *Palaechthon*, *Palenochtha*, and *Torrejonia*) lists the notch between the hypoconulid and entoconid—a feature absent from M_{1-2} of the four latter genera. They regard *Plesiolestes* and *Palaechthon* ancestral to *Microsyops* and *Craseops*, whereas *Palenochtha* is considered basal to the uintasoricine microsyopids. This phylogenetic scheme would require parallel loss of the protocone fold and hypoconulid-entoconid crest and parallel appearance of a hypocone, twinned hypoconulid-entoconid, and a notch between the latter in the evolution of the two subfamilies of microsyopids—not an impossible occurrence, but perhaps not the most cogent interpretation of the dental evidence.

Apart from these difficulties, the suggestions of a close relationship among some paromomyids, uintasoricines, and microsyopines are not based on shared-derived characters but on an amalgam of primitive features and stratigraphic occurrences. All tarsiiforms, including uintasoricines (Fig. 1, node 3) have parabolic protocristae on M^{1-3}. All plesiadapiforms, including paromomyids (Fig. 1, node 5), have a protocone fold on M^{1-2}. Microsyopids (*Microsyops*, *Craseops*, *Navajovius*, *Alsaticopithecus*) lack these derived features and are not closely related to uintasoricines or paromomyids. Furthermore, the hypoconulid and entoconid in uintasoricines are not "twinned" in the sense that they are in microsyopids, marsupials, bats, or nyctitheriids. Because the hypoconulid in uintasoricines is a low, elongate thickening on the hypocristid, its lingual tip occurs near the entoconid. The supposed twinning is an artefact of the compression and lingual elongation of the hypoconulid.

Uintasorex Matthew, 1909

Uintasorex sp. cf. U. parvulus Matthew, 1909

No additional teeth of *Uintasorex* have been recovered since Robinson (1968) recorded the occurrence of this primate at Badwater. Like *U. parvulus*, but unlike the Uintan *U. montezumicus* (Lillegraven, 1976) the isolated upper molars have weak posterior cingula that lack a hypocone.

Summary and Conclusions

Seven species of primates are recorded from the late Eocene Badwater deposits: *Phenacolemur mcgrewi*; *P. shifrae* (Paromomyidae);

Chumashius sp.; *Macrotarsius siegerti*; *Mytonius hopsoni* (Omomyinae); *Uintasorex* sp. cf. *U. parvulus* (Uintasoricinae); *Trogolemur* sp. (Anaptomorphidae). The occurrence of late Eocene *Phenacolemur*, multituberculates, a high proportion of eomyid rodents, a dermopteran, certain insectivores, and selenodont artiodactyls (Krishtalka and Black, 1975; Krishtalka and Setoguchi, 1977; Black, 1978; M. R. Dawson, personal communication) implies that certain levels in the Badwater sediments preserve a unique Uintan-Duchesnean facies—not the lowland, intermontane basin situation of most Eocene localities but, predominantly, a drier, upland, savannah woodland environment with restricted pockets of riverine, forested habitat.

Among the taxa discussed in this paper, *Phenacolemur* and *Ignacius* are provisionally maintained as separate genera, although *I. mcgrewi* is referred to *Phenacolemur*. *Ourayia* is not known from the upper dentition but includes only the holotype and associated partial dentaries from the Uintan of Utah. The palate and associated dentaries formerly assigned to *Ourayia* (Simons, 1961; Szalay, 1976) and *Hemiacodon* (Robinson, 1968) are indistinguishable from *Macrotarsius* and comprise the type of *M. jepseni* from the Uintan of Utah. *Mytonius hopsoni* is tentatively recognized because the referred material, although sparse and fragmentary, differs significantly from the known sample of *Ourayia*.

New hypotheses of relationships among and generic composition of the major groups of plesiadapiform-tarsiiform primates are depicted in Fig. 1 and defined by inferred shared-derived characters. If these are correct, the Anaptomorphiade and Omomyidae as most recently reviewed by Szalay (1976) are unnatural groups. Contrary to Szalay's (1976:277, 280) conclusion, absence of a protocone fold on upper molars of "*Ourayia*" (=*Macrotarsius jepseni*) is not a specialization among omomyids, but a retained primitive condition of all tarsiforms. The presence of a protocone fold among some plesitarsiiforms is one of the derived characters that implies their common ancestry—a relationship expressed taxonomically by the clade Plesiadapiformes (Fig. 1, node 5). Accordingly, this clade includes not only plesiadapids, carpolestids, and paromomyids (Gingerich, 1976) but also anaptomorphids and microchoerids (revised; see Fig. 1 for included genera). Cladistically, the Plesiadapiformes is a sister group of the Tarsiiformes, which only include omomyids (Omomyines and uintasoricines; revised, see Fig. 1 for included genera). They lack a protocone fold, but the protocristae on the upper molars are much more divergent and form a broad parabola enclosing a larger trigon basin (Fig. 1, node 3).

Accordingly, among the taxa discussed here, *Macrotarsius, Omomys, Chumashius,* and *Uintasorex* are tarsiiforms. *Ourayia* and *Mytonius*, known only from the lower dentition, are tentatively included

in the Omomyidae on the basis of derived features on P_5–M_2 shared with *Macrotarsius*. *Hemiacodon*, with a strong protocone fold on M^{1-2}, is not an omomyid (*pace* Szalay, 1976), but, along with *Washakius*, *Shoshonius*, and *Loveina*, is a member of the Washakiinae, a subfamily of Anaptomorphidae (Fig. 1, nodes 7, 7B). On M^{1-2} of these four genera the postprotocrista is short, the pre- and postcingular end lingually in a pericone and hypocone, respectively, and the protocone fold-postcingulum junction is weak but marked by a tiny cuspule or wear facet.

A more detailed synthesis of the relationships among described plesiadapiform-tarsiiform genera will appear elsewhere (Krishtalka and Schwartz, manuscript), along with a discussion of omitted taxa and synonymies.

ACKNOWLEDGMENTS

LITERATURE CITED

Black, C. C. 1967. Middle and late Eocene mammal communities: a major discrepancy. Science, 156:62–64.

———. 1978. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 14. The artiodactyls. Ann. Carnegie Mus., 47:223–259.

Bown, T. M., and P. D. Gingerich. 1972. Dentition of early Eocene primates *Niptomomys* and *Absarokius*. Postilla, 158:1–10.

———. 1973. The Paleocene primate *Plesiolestes* and the origin of Microsyopidae. Folia Primat., 19:1–8.

Bown, T. M., and K. D. Rose. 1976. New early Tertiary primates and a reappraisal of some Plesiadapiformes. Folia Primat., 26:109–138.

Clark, J. 1941. An anaptomorphid primate from the Oligocene of Montana. J. Paleontol., 15:562–563.

Gazin, C. L. 1958. A review of the Middle and Upper Eocene primates of North America. Smithsonian Misc. Coll., 136:1–112.

———. 1968. A new primate from the Torrejon Middle Paleocene of the San Juan Basin, New Mexico. Proc. Biol. Soc. Washington, 81:629–634.

———. 1971. Paleocene primates from the Shotgun Member of the Fort Union Formation in the Wind River Basin, Wyoming. Proc. Biol. Soc. Washington, 84:13–38.

Gingerich, P. D. 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). Univ. Michigan Papers Paleontol., 15:1–140.

Krishtalka, L., and C. C. Black. 1975. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 12. Description and review of late Eocene Multituberculata from Wyoming and Montana. Ann. Carnegie Mus., 45:287–297.

Krishtalka, L., and J. H. Schwartz. MS. Phylogenetic relationships among the plesiadapiform-tarsiiform primates.

Krishtalka, L., and T. Setoguchi. 1977. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 13. The late Eocene Insectivora and Dermoptera. Ann. Carnegie Mus., 46:71–99.

Lillegraven, J. A. 1976. Didelphids (Marsupialia) and *Uintasorex* (?Primates) from later Eocene sediments of San Diego County, California. Trans. San Diego Soc. Nat. Hist., 18:85–112.

Matthew, W. D. 1909. The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. Mem. Amer. Mus. Nat. Hist., 9:289–567.

———. 1915. A revision of the Lower Eocene Wasatch and Wind River faunas. Part 4. Entelonychia, Primates, Insectivora (part). Bull. Amer. Mus. Nat. Hist., 34:429–483.

Matthew, W. D., and W. Granger. 1921. New genera of Paleocene mammals. Amer. Mus. Novitates, 13:1–7.

McKenna, M. C. 1960. Fossil Mammalia from the early Wasatchian Four Mile Fauna, Eocene of northwest Colorado. Univ. California Publs. Geol. Sci., 37:1–130.

Osborn, H. F. 1895. Fossil mammals of the Uinta Basin. Expedition of 1894. Bull. Amer. Mus. Nat. Hist., 7:71–105.

———. 1902. The American Eocene primates and the supposed rodent family Mixodectidae. Bull. Amer. Mus. Nat. Hist., 16:169–214.

Robinson, P. 1968. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 4. Late Eocene primates from Badwater, Wyoming, with a discussion of material from Utah. Ann. Carnegie Mus., 39:307–326.

Schwartz, J. H. 1979. Dental development, homologies and primate phylogeny. In press.

Schwartz, J. H., and L. Krishtalka. 1976. The lower antemolar teeth of *Litolestes ignotus*, a late Paleocene erinaceid (Mammalia, Insectivora). Ann. Carnegie Mus., 46:1–6.

———. 1977. Revision of Picrodontidae (Primates, Plesiadapiformes): dental homologies and relationships. Ann. Carnegie Mus., 46:55–70.

Simons, E. L. 1961. The dentition of *Ourayia*: -its bearing on relationships of omomyid prosimians. Postilla, 54:1–20.

———. 1972. Primate evolution: an introduction to man's place in nature. Macmillan Co., New York, xii + 322 pp.

Simpson, G. G. 1955. The Phenacolemuridae, new family of early primates. Bull. Amer. Mus. Nat. Hist., 105:411–442.

Stock, C. 1933. An Eocene primate from California. Proc. Nat. Acad. Sci., 19:954–959.

Szalay, F. S. 1969a. Mixodectidae, Microsyopidae, and the insectivore-primate transition. Bull. Amer. Mus. Nat. Hist., 140:193–330.

———. 1969b. Uintasoricinae, a new subfamily of early Tertiary mammals (?Primates). Amer. Mus. Novitates, 2363:1–36.

———. 1973. New Paleocene primates and a diagnosis of the new suborder Paromomyiformes. Folia Primat., 19:73–87.

———. 1975. Phylogeny of primate higher taxa: the basicranial evidence. Pp. 91–125, *in* Phylogeny of the primates (W. P. Luckett and F. S. Szalay, eds.), Plenum Press, New York, xiv + 483 pp.

―――. 1976. Systematics of the Omomyidae (Tarsiiformes, Primates) taxonomy, phylogeny, and adaptations. Bull. Amer. Mus. Nat. Hist., 156:157–450.

West, R. M., M. C. McKenna, C. C. Black, T. M. Bown, M. R. Dawson, D. J. Golz, J. A. Lillegraven, D. E. Savage, and W. D. Turnbull. MS. Eocene biochronology of North America.

Wortman, J. L. 1904. Studies of Eocene mammals in the Marsh Collection, Peabody Museum. Amer. J. Sci., ser. 4, 17:23–33, 133–140, 203–214.